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NUMBER 2

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BREATHING LIFE INTO FOSSILS:

Taphonomic Studies in Honor of C.K. (Bob) Brain

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COVER CAPTIONS AND CREDITS.

Front cover, clockwise from top left.

Top left:
Artist's reconstruction of the depositional context of Swartkrans Cave, South Africa, with a leopard consuming a hominid carcass in a tree outside the cave: bones would subsequently wash into the cave and be incorporated in the breccia deposits. © 1985 Jay H. Matternes.

Top right: The Swartkrans cave deposits in South Africa, where excavations have yielded many hominids and other animal fossils. ©1985 David L. Brill.

Bottom right: Reconstruction of a hominid being carried by a leopard. © 1985 Jay H. Matternes.

Bottom left: Photograph of a leopard mandible and the skull cap of a hominid from Swartkrans, with the leopard's canines juxtaposed with puncture marks likely produced by a leopard carrying its hominid prey. © 1985 David L. Brill.

Center: Photo of Bob Brain holding a cast of a spotted hyena skull signed by all of the taphonomy conference participants. © 2004 Kathy Schick, Stone Age Institute.

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CHAPTER 6

TAPHONOMY AND SITE FORMATION OF TWO EARLY MIOCENE SITES ON RUSINGA ISLAND, KENYA

ALAN WALKER

ABSTRACT

Many Early Miocene sites on Rusinga Island, Kenya, have produced fossils of the stem ape *Proconsul*. Two of them have unusual taphonomic histories. One, R114, that contained the type specimen of *Proconsul heseloni*, is the infilling with matrix and bones of a large hollow tree trunk. The other, the Kaswanga Primate Site, is either a small channel fill or the remains of an infilled carnivore burrow that was dug into soft sediment.

INTRODUCTION

Thomas Whitworth (1953) found the R114 site while mapping the geology of the Gumba peninsula on the Southwest of Rusinga Island in Lake Victoria, Kenya. Louis Leakey and his associates excavated there in 1950 and removed large blocks of matrix. These contained parts of a *Proconsul* skull and associated bones of a forelimb and foot that were the subject of analysis by Napier and Davis (1959). Subsequently, parts of the same individual were found unidentified in the Kenya National Museum (Walker and Pickford, 1983). That discovery led to Johns Hopkins University/National Museums of Kenya expeditions from 1984-1988 to understand the taphonomic and sedimentary context and to search for more *Proconsul* bones. More were indeed found and the partial skeleton became the type of a new species, *P. heseloni* (Walker et al., 1993).

A new site was also discovered while prospecting in the first year of these expeditions. It contained several partial *Proconsul* individuals and was named the Kaswanga Primate Site. Only brief accounts of the sites have been published so far (Walker et al., 1986; Walker and Teaford, 1988), but some of the history behind them has been given (Walker, 1992; Walker and Shipman, 2005). This account expands on those. Figure 1 shows the locations of the sites on Rusinga Island.

SITE R114

Whitworth was asked by Louis Leakey to make a geological map of the Gumba Penninsula, the Western part of Rusinga Island that lies in the Winam Gulf of Lake Victoria. This is centered about 34^o 6’ East and 0^o 25’ South. In August 1950, he found site R114 which he described in his notes as “a tiny and isolated outcrop,” and in his publication as “a small circular pipe,” penetrating the flaggy Series (Whitworth, 1953). In the article he went on to say, “The profusion of articulated skeletons found in this limited deposit suggest [sic] that it may represent the infilling of a pothole in which animals were trapped.” (Whitworth, 1953: 91). Napier and Davis (1959) in their monographic account of the *Proconsul* bones from the site, elaborated on this by suggesting that “the pot-hole may have acted as a trap for unwary animals that came there to drink.” When Pickford and Walker found more parts of the same skeleton in the National Museum of Kenya that had been unidentified or misidentified, a search was made to find the site again (Walker and Pickford, 1983).

A preliminary exploration of the depositional environment by Pickford was published in that paper, but his results have been superseded by subsequent expeditions, so hardly anything in that account is correct. Although he recognized that the fossil deposit was not well exposed, he thought that the grit of which it was composed

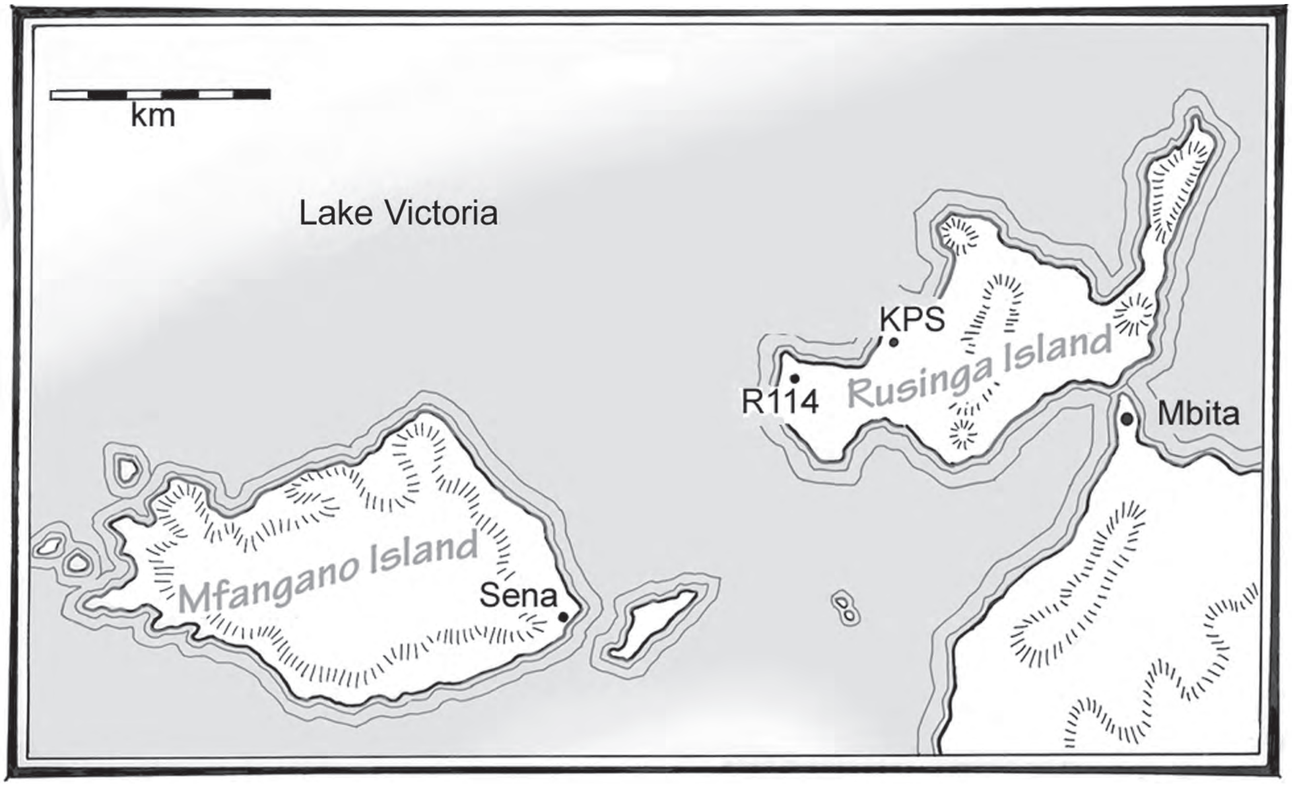

Figure 1. Map of Rusinga and Mfangano Islands in the eastern part of Lake Victoria, Kenya, to show the locations of sites R114 and the Kaswanga Primate Site (KPS).

"overlays a clay drape which thickens laterally where it contains a tragulid skeleton." The deposit proved to cut through the country rocks, rather than resting on them and the tragulid, which had no association with the deposit, turned out to be a springhare, *Megapedetes pentadactylus*. He further wrote, "the deposit was about 10 × 5 m in extent and about 0.3–0.5 m thick, with a gently sloping basal profile." The account of the taphonomy given by Walker and Pickford is likewise incomplete, but the observations are now seen with hindsight, to be mostly correct. Among the peculiarities noted then were: most fossils occurred as articulated or semi-articulated specimens with little or no mixing of bones from different individuals. The arms bones of *Proconsul*, though removed from the matrix in Leakey's time, were clearly articulated when buried and, like other parts of the skeleton including the lower incisors, warped *in situ*. It was also noted that the larger animals were juveniles while the small mammals were adult. And last, there was carnivore damage to the *Proconsul* skeleton. This can be seen by an obvious tooth marks on the proximal metaphysis of the right femur and the tibial articular surface of the right talus, and gnawing of the calcaneal tuber on the right calcaneum. Other possible tooth marks are present on other bones, but the crude preparation by hammers and nails in the early 1950s made most of them ambiguous.

Beginning in 1984, the site was cleaned up and many more blocks of rock with bones were found scattered around the area. These included more of the same subadult *Proconsul* skeleton. All blocks around the site and downslope of it were collected, washed and inspected. Bones showing on the surface of the blocks were extracted using Airscribes (Chicago Pneumatic Corp.,) powered by a gas powered air compressor on site. Those blocks without bones showing on the surface were broken down into smaller ones until they were either too small to contain mammal bones, or had bones within them. In this way more bones of the *Proconsul heseloni* type specimen were found (Walker et al., 1986).

The site was cleaned to reveal the situation that Louis Leakey and his associates left in 1950. The circular "pipe" was an obvious 1 m diameter feature in the center of a shallow depression excavated in the flaggy series. The excavators had made us of planes of slickensides to remove the country rock around the "pipe" and these were plotted for aximuth and dip. All the planes were dipping between 39^o to 50^o towards the center of the "pipe". When allowance is made for the regional dip, these all convert to almost exactly 45^o. The circular "pipe" of Whitworth was still to be seen as a greenish, fenitized rock surrounded by grey volcanoclastic flagstones. Fenite is a metasomatically altered quartzo-feldspathic rock comprising mainly alkali feldspar and aegirine augite, and is common around carbonatite volcanos such as Kisingiri. Its typical green color made separation of the "pipe" rock from others very easy. Excavation of a wedge of flagstones down the outside of the "pipe" was undertaken and, when work was stopped in 1984, showed the "pipe" extending downwards into the country rock for at least 3 m. The country rock was asymmetrically deposited around the "pipe," with fine strata on one side and coarser rock with occasional pebbles on the south side. Figure 2 is a photograph of the "pipe" infilling, and shows that the infilling itself is coarsely stratified and that the flaggy series sedimentation was affected by the structure that the "pipe" represents.

These observations refuted the "pothole" theory and led to the conclusion that the structure that created the "pipe" was standing when the flaggy series rocks were deposited, and there are no obvious geological structures that also could contain bones that could be in that configuration. Further, several other, smaller vertical features were found in the Hiwegi Formation, some nearby site R114, and some also containing bones. Several of these had basal features that were clearly calcite-filled buttress roots of trees, and although the excavation at R114 did not reach the base of that infilling, that too was obviously the infilling of a large, hollow tree trunk. The pattern of slickensides also explained some of the distortion of bones, including the peculiar state of the original forelimb skeleton, whereby the arm was folded in its flexed death position so that both radius and humerus were bent in the same way. The sediment filling the hollow tree was initially loosely packed, whereas the surrounding flagstones were water deposited and were more rigid. Subsequent compression of the cylindrical infilling produced cone-in-cone faults with slickensides in the country rock immediately next to the tree at 45^o. In another infilled tree site nearby, these cone-in-cone faults are seen to be both downwards and upwards, but at the R114 site the excavators had, naturally, only made us of the downward planes.

With the site established as the infilling of a hollow tree, several points are cleared up. First, the concentration of partial or nearly complete skeletons in a small area is clearly the result of animals being carried in or using the tree as a roost. Walker and Pickford (1983, Table 1) published a faunal list from the R114 site, and this has been added to with a large molossid bat, and a virtually complete tragulid skeleton. Roosting is almost certainly the case with the newly described bat species *Tadarida rusingae* (Arroya-Cabrales, et al., 2002), the python and monitor lizards (Walker and Pickford, 1983), and at least one of the three carnivore species that left tooth marks on the *Proconsul* skeleton. The 15 *Paraphiomys* rodent skeletons might also represent animals that used the tree when they were alive. A mammalian carnivore, probably a hyaenodontid creodont, is the most likely collection agent for the *Proconsul*, the seven small artiodactyls, five rabbit and one mole rat skeletons. Most of the larger skeletons were immature but the smaller mammals were adult, another point that supports the carnivore collection possibility. Although a detailed examination of all of the bones from this site has not yet been made, it seems as though the taphonomic history was a complex one, with a large tree becoming hollowed, probably after its death following the burial of the lower part by volcaniclastic sediments. Animals roosted in the hollow tree and were preserved in sediments filtering down from the upper surface of the newly deposited sediments. Similarly, animals brought in whole or in parts by carnivores would accumulate with the sediments trickling in from above. Second, the time elapsed for the hollow tree to be filled with sediment cannot have been very long. This means that the animals were part of the same community that lived in the immediate area and were not brought together in a "pothole" by stream action that might have been capturing runoff from large distances upstream. Third, this also means that the fauna is not any different in geological age from that of the rest of the Hiwegi Formation, as it might have been had a pothole formed much later than the hardened sediments into which it was cut. Record keeping by Louis Leakey during the collection of the original blocks from R114 was minimal. We know that the infilling stood out from the flaggy series as a low pillar and that Leakey and his colleagues broke this up into blocks (Walker, 1992). That several blocks that contained Proconsul bones were left on site, probably means that Leakey could have collected all of the skeleton had he taken more care. He, or others, also failed to recognize parts of the skeleton during preparation and we know, as was the case of the left first metacarpal that still had an old glue join on it, that parts have also been lost over the years.

Attempts have been made to recover more blocks of the infilling for preparation, and this has been successful in the

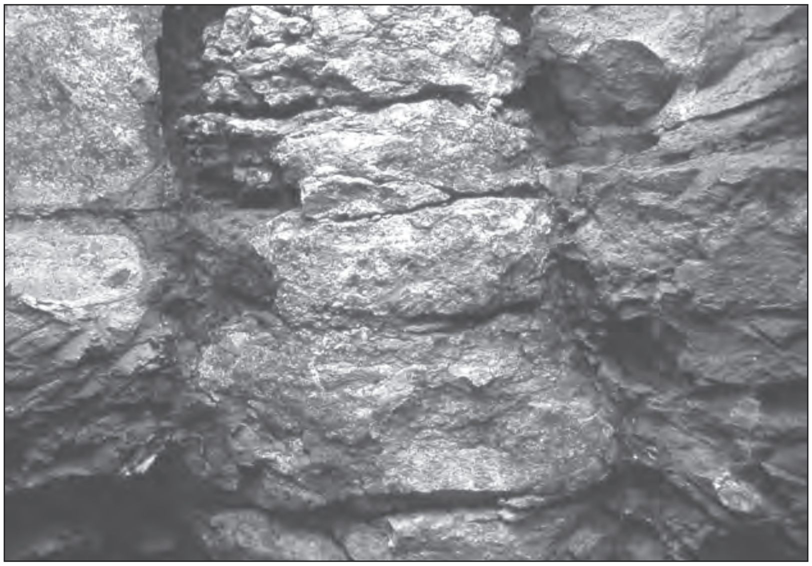

Figure 2. Photograph showing the infilled tree at R114 as viewed from a wedge-shaped trench excavated through the flaggy series surrounding it. Note that the infilling widens downwards and is stratified. Also note that the flaggy series beds are asymmetrical with respect to the infilling, showing that the tree acted to influence their sedimentation.

case of a tragulid skeleton that has yet to be described. Much more remains to be done at this site. Some recovered blocks were unintentionally used to fill in potholes in the roads of the Museum grounds. More bones would certainly be found without undue time expenditure by staff if an acid preparation system such as that in use at the Transvaal Museum in Pretoria, South Africa, were started in Nairobi.

THE KASWANGA PRIMATE SITE

The site was discovered by Bwana Peter Nzube in 1984. The site is located on the northern set of exposures at Luanga near Kaswanga and is about 110 meters ESE of the Kenya Government meteorological station. It lies approximately 34°09' East, 0°24' South. Figure 3 shows its location relative to the regional geology. This area is part of site R5 of Andrews and Van Couvering, (1975) and Pickford (1986). The site number R5 was originally given by Le Gros Clark and Leakey (1951) to a "Red Band in upper part of Kathwanga Series" at Luanga. Additional numbers (30-40 and 80-89) referred to sites in the "upper and lower parts of the Kathwanga series," but none of them was ever used afterwards (J. A. Van Couvering, personal communication, 1988). Fossils collected on our expeditions are recorded on enlargements of aerial photographs that are kept in the Palaeontology Department of the National Museum of Kenya, so numbers for individual sites are not needed. Van Couvering and Miller (1969) give an account of the geology and dating of Rusinga Island with further details of the Kaswanga stratigraphy presented by Van Couvering (1972). Observations on the general geology and comments on the Kaswanga sites are given by Pickford (1986). The most recent geochronological studies of Rusinga (Drake et al., 1988), suggest that these deposits are of later Early Miocene age, about 17.8 million years old, significantly younger than those of Songhor and Koru.

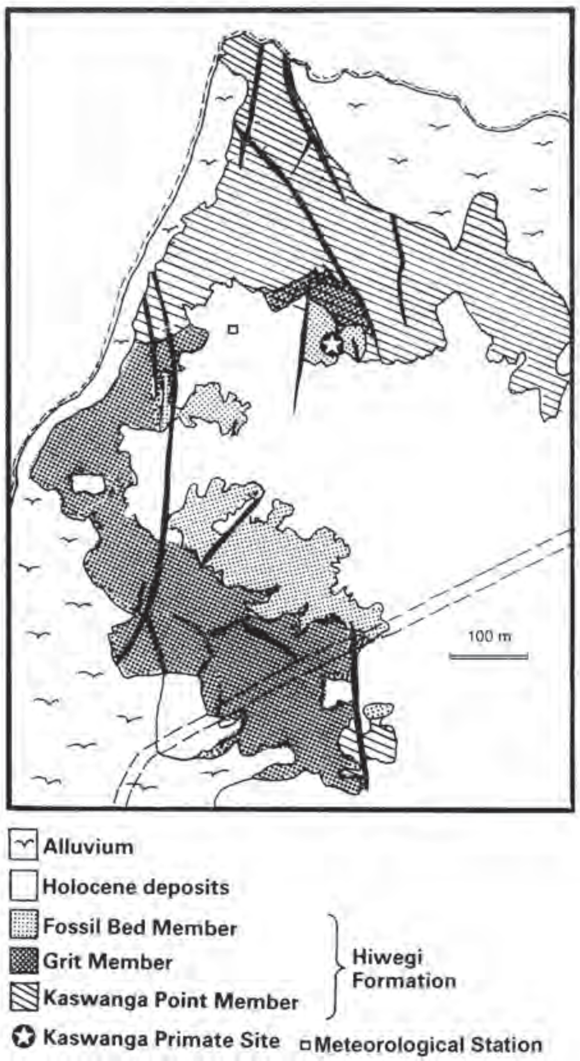

Figure 3. Geological map of the Kaswaga area, Rusinga Island.

The lower Hiwegi Formation forms the primary exposure in the area around the site. The excavation and detailed stratigraphic observations carried out in 1985 show that the fossils come from an infilling of Fossil Bed Member silts into a steep but shallow (1 m deep) channel or burrow cut into the underlying Grit Member of the Hiwegi Formation (Van Couvering and Miller, 1969). A topographic map of the site was made to 5 cm contours. This fine level of height resolution showed the disconformity between the two sedimentary units. The map and the local geology are shown in Figure 4. The sediments of the Grit Member either had a primary dip of about 4° to the northeast or were tilted in that direction before the channel or burrow was formed. It is difficult to prove that the feature was a burrow as the infilling matrix with bones is the identical to the surrounding rock, except for being less compacted, and because it seems that the roof of the burrow, if it was one, has long been eroded away. The features were then filled with fine-grained tuffaceous silts and clays that contained *Proconsul* remains, a very few other small mammal bones, leaves and fruits. The leaves and fruits are only found in the tops of the channel feature, but *Proconsul* bones are found throughout. The channels were probably filled in one, very brief, possibly slumping, episode, but the silts and clays point to it being a low energy sedimentary environment. As a result a few hominoid body parts were still in articulation when the original discovery was made. Although many bones were excavated from the depths of the feature, these were all disarticulated and their epiphyses were also found separated. There is no good reason at present to imagine anything other than post-mortem association between the individuals.

The first work at the site in 1984 consisted of collecting the surface bones and teeth that had weathered out. These included the two adult foot skeletons and the hand bones of Individual III and the infant leg and foot bones of Individual IV. Some of the loose surface soil and sediment was carried to Lake Victoria and water washed through screens of mosquito netting. Many bones and teeth were recovered in this way. The site was secured with a fence to prevent further disturbance until excava-

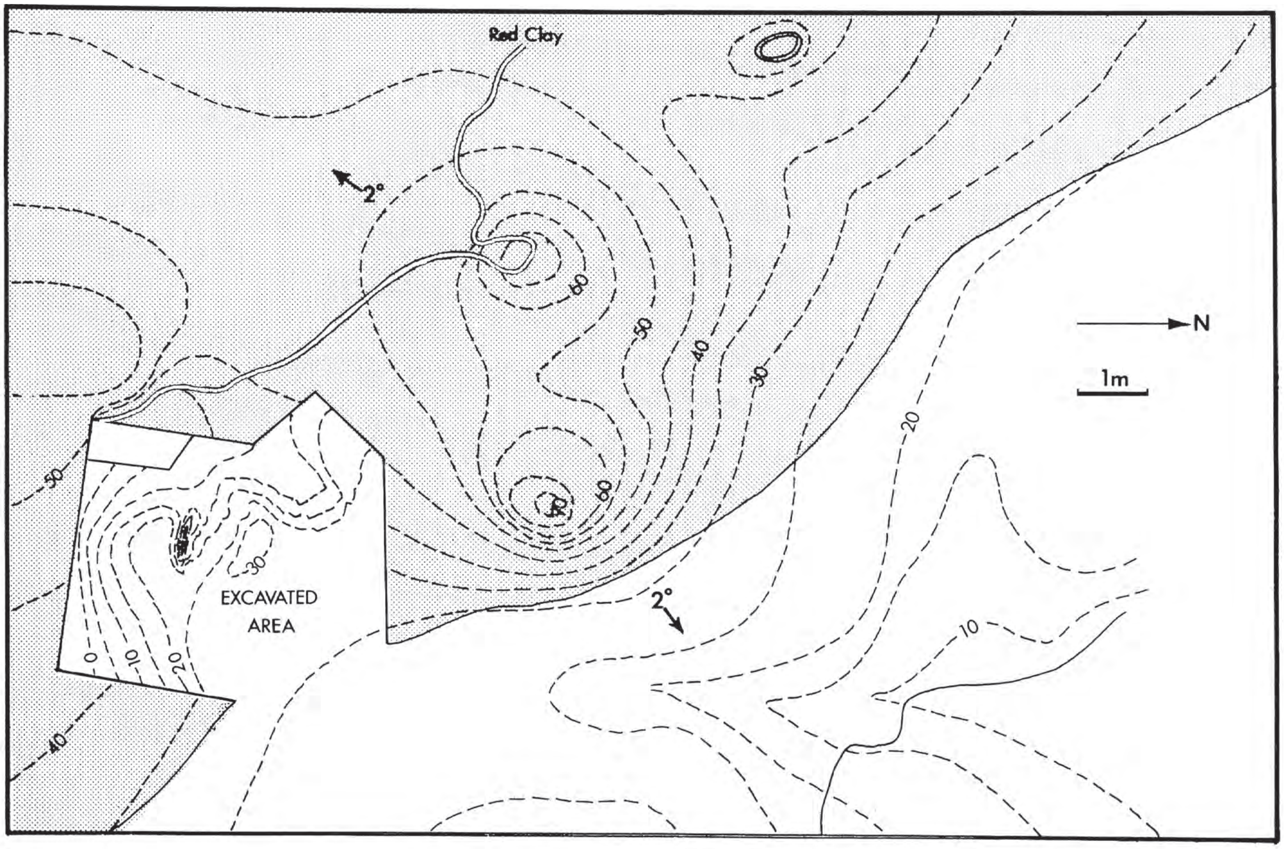

Figure 4. Geological map of the Kaswanga Primate Site.

tion could be started in 1985. Once again surface soil and sediment was water washed and excavations begun. Bones were found *in situ*, mainly to the west of the position of the adult foot skeletons, and their 3-D positions plotted. It is important to emphasize that a soil profile had developed across the site. Also that the similarity of filling material with bones to the surrounding sediment meant that the limits of the channel or burrow were better felt than seen. Bones were not found in hard, very consolidated tuffaceous sediment. They always occurred in softer, less consolidated rock. Subsequent sorting of the disarticulated bones that were excavated revealed the presence of only two individuals, one subadult, presumed male, mostly complete and the other, larger subadult male only represented by a few parts. This immediately suggested that the bones and sediment had mixed together while the feature was filling. Figure 5 is a site plan showing the excavated bones and those that were still in situ at the start of cleaning.

Orientation of the excavated bones at the site was limited to those that had a suitable shape and length. As the two individuals excavated were disarticulated subadults, all of their epiphyses were isolated, leaving shortened diaphyses that in some cases were distorted or broken. For the 27 bones for which good orientation measurements were collected, there is a consistent non-random trend that can be seen in the mirror-image rose diagram (Figure 6). A quarter (n = 7) of the bones were oriented between North and 20^{o}. Nearly half the bones (n = 12) were oriented between North and 40^{o}. These bones were sampled from all depths in the deposit and so this marked overall trend probably results from movement of the unconsolidated sediment body that already had disarticulated bones dispersed within it. This is in contrast to the articulated skeletons foot and leg skeletons of Individuals III and IV, for not only are they articulated, but the tibias of them were oriented at 75^{o} and 145^{o} respectively. It is very probable that the rest of these two skeletons were completely articulated before the site was eroded, and further, that if they has been moved in a sediment body they had been moved intact. Indeed, the position of the articulated hand skeleton of Individual III was found where it might have been expected had the articulated skeleton been complete. It is possible that careful examination of bones of those individuals that were not found *in situ* would show, through adjacent similar distortion or manganese dioxide dendritic staining, that they had lain together in the deposit.

The individual *Proconsuls* from the Kaswanga Primate Site were sorted by several means. Lower legs and feet of two of them were articulated *in situ*. This meant that these individuals (III and IV) could have other pieces glued to them that were recovered by screening or washing. Others had bones assigned to them by size, color, manganese dioxide staining patterns, age state, congruency of articulations or interstitial facets, and mirror-imaging. There still are hundreds of small pieces of bone that have not been assigned to individuals and these include 42 phalanges (Begun et al., 1994), and over 20 metapodials or parts of them. The difficulty is some-

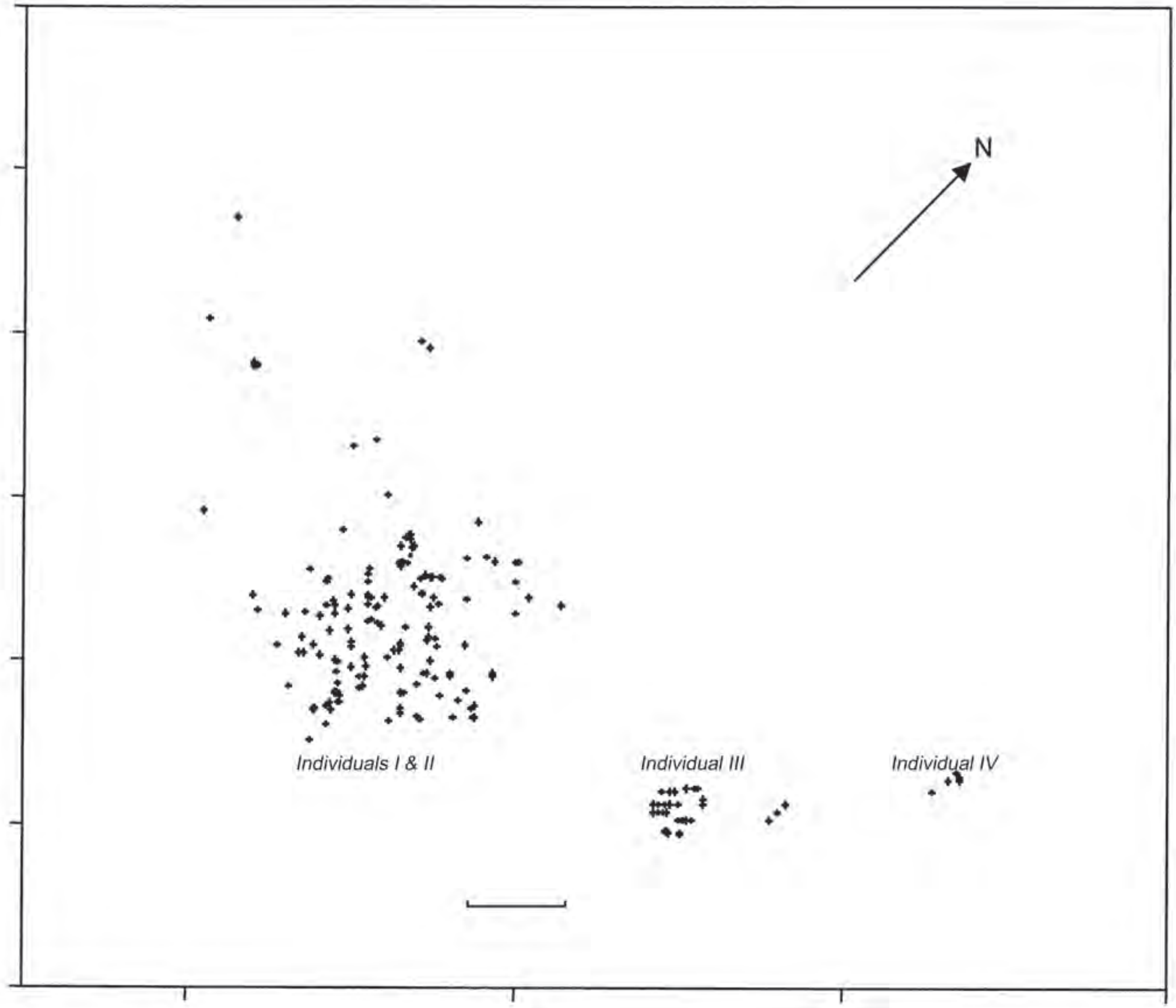

Figure 5. Plot of the excavated part of the Kaswanga Primate Site from 3-D coordinated data. The positions of the excavated bones of Individuals I and II and the in situ lower leg and foot skeletons of Individuals III and IV. The scale bar represents 25 cm. Note that many points are plotted over each other.

times made more difficult because we cannot tell which body part pieces are (e.g., a small cylindrical juvenile fibular fragment may be confused with an adult cylindrical metapodial one). Also, many of the bones are bent or otherwise distorted, sometimes misleading even experienced paleontologists. This was the case when Harrison (1998) decided that two specimens identified by me as lumbar vertebrae were in fact caudal ones. This misidentification presumably came about because although one of them (specimen V9) is half of a lumbar body, it is also distorted, and because although specimen V10 is a whole lumbar body, it too is distorted. Detailed study of these two bones (Nakatsukasa et al., 2004) shows quite clearly that the original identification was correct. It is still a concern that we made mistakes in attributing parts to individuals. For instance, it seems certain that two subadult males were mixed together in the part of the site that could be excavated. One of these has most of the skeleton preserved while the other has only a few scraps. Note particularly that we assigned a set of isolated lower teeth to one and a set of isolated uppers to another. This deserves a more thorough assessment as it could be that most of the bones belong to Individual I, and only a very few parts such as the distal end of a fibula, to Individual II.

The numbering of individual parts and individuals was a particular concern that has yet to be satisfactorily resolved. Standard practice at the National Museum of Kenya has been to write a unique identifying number on the specimen. This, for historical reasons, is preceded by a museum and site identifier, e.g., KNM-SO for Songhor, KNM-RU for Rusinga, although such crude site definitions have long given way to detailed site information, such as the field numbers written on the back of the relevant air photographs. The unique numbering system has for many years now been solidly in 5 figures for Department of Paleontology specimens. For those specimens with many isolated body parts the practice has been to

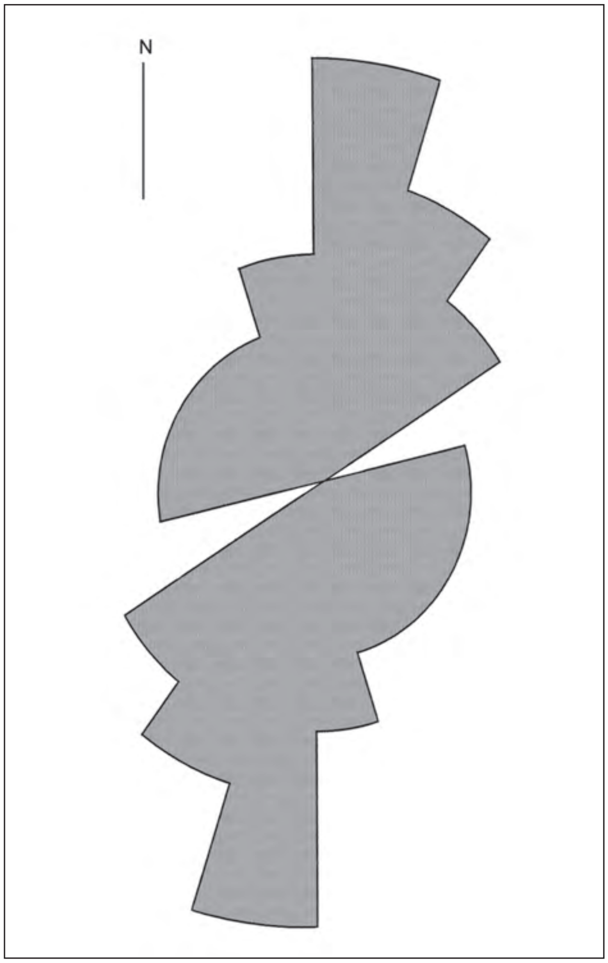

Figure 6. Mirror-image rose diagram of 27 oriented bones excavated at the Kaswanga Primate Site.

add a letter suffix, e.g., the type of *Proconsul heseloni*, KNM-RU 2036 has so many isolated bones that the suffixes have long since passed one alphabet, and so another letter has been added—e.g., the left tibia is KNM-RU 2036BA. To write a Museum Accession Number on Kaswanga Primate Site bones we would have to write a 13 digit number such as KNM-RUXXXXXAG. To put this on some large long bones might be possible, if unaesthetic, but to write such a number, as well as our field identifiers on tiny infant hand or foot bones would be virtually impossible. A scheme to use microdot numbers that could be glued on a specimen and read under a binocular microscope was not attractive to grant reviewers. So to date, only our field identifiers remain written on the bones. These are numbers that follow a letter code for body part (R for radius, P for pelvis, etc.) For ease of sorting and keeping track of material, we have added small water-soluble colored dots to each bone that we have given to a particular individual. These are as follows: Individual I–bright pink, Individual II–gold, Individual III–purple, Individual IV–blue, Individual V–dark green, Individual VI–yellow, Individual VII–red, Individual VIII–light green, Individual IX–maroon, Individual X–white. Figure 7 shows the individuals are constituted now. Hundreds more parts remain to be sorted.

KPS individual I – subadult male

Teeth: Left I^1, fragment of incisor root, incisor root and bit of crown left I^2, left P^3, left P^4, right P^4 , left M^{1-3}, right M^1, right M^3.

Skull: Sk 2 – petrous temporal

Axial Skeleton: Tl – sternebra, RB3 – right first rib, RB1 – rib fragment, VI – vertebral lamina, V2 – vertebral body, V3 – vertebral body, V44 – vertebral body, V45 – lamina + part of spine and left lower articular process, V90-V96, V98 – misc. vertebral fragments, V97 – vertebral body.

Forelimb: HI – right distal half of humerus shaft, El – right capitular epiphysis, R2 – distal shaft of radius, proximal end (?left) radius, E3 – radial epiphysis, fragment of ulnar styloid, C10 – right pisiform (damaged), C3 – right capitate (damaged), C9 – Triquetrum, E4 – scaphoid tubercle, C48 – left trapezium (identified originally by Beard et al. (1986) as right trapezoid), C4 – left capitate (damaged), Cl – left centrale, C8 – left scaphoid, T14 – right trapezium, C6 – left hamate (damaged), C5 – left lunate (damaged), MT15 – right metacarpal 1, MT13 – right metacarpal II, MT9 – right metacarpal III, MT16 – right metacarpal IV, MT11 – right metacarpal V, MH1-MH12 – metapodial epiphyses, PH9 proximal phalanx ray 4, PH10 proximal phalanx ray 4, PH11 proximal phalanx ray 5, PH19 left proximal phalanx ray 1, PH21 proximal phalanx ray 3, PH24 proximal phalanx ray 2, PH37 proximal phalanx ray 3, PH26 middle phalanx ray 3, PH36 middle phalanx ray 4, PH96 terminal phalanx ray 1, 25 Phalangeal epiphyses.

Pelvis/Hindlimb: PI – right pubis, P17 – right ischium, P2 – left pubic ramus, P18 – left ischium, Fl – left femur, F2 – right femur, E45 – right distal epiphysis of femur, TB1 – left tibia, TB2 – anterior crest of (?left) tibia fragment, E44 – proximal epiphysis of left tibia, E9 - distal epiphysis of left tibia, E7 – distal epiphysis of right tibia, Rl – left fibula shaft fragment, FB3 – distal fibula (shaft), E8 - distal end of left fibula, T13 – right calcaneum, T11 – right talus, T3 – right cuboid, T16 – left lateral cuneiform, T5 – right navicular, T12 – left calcaneum, T10 – left talus, T6 – left navicular, T4 – left cuboid, T9 – left medial cuneiform, T7 – right medial cuneiform, MT14 – right metatarsal I, MT12 – right metatarsal II, MT4 – right metatarsal III, MT6 – right metatarsal IV, MT3 – right metatarsal V, MT2 – left metatarsal I, MT8 – left metatarsal II, MT5 – left metatarsal III, MTI – left metatarsal IV, PH1 left proximal phalanx ray 5, PH4 right proximal phalanx ray 4, PH6 left proximal phalanx ray 4, PH7 right proximal phalanx ray 4, PH8 left proximal phalanx ray 2, PH13 right proximal phalanx ray 1, PH25 left proximal phalanx ray 1, PH2 middle phalanx ray 2, PH15 middle

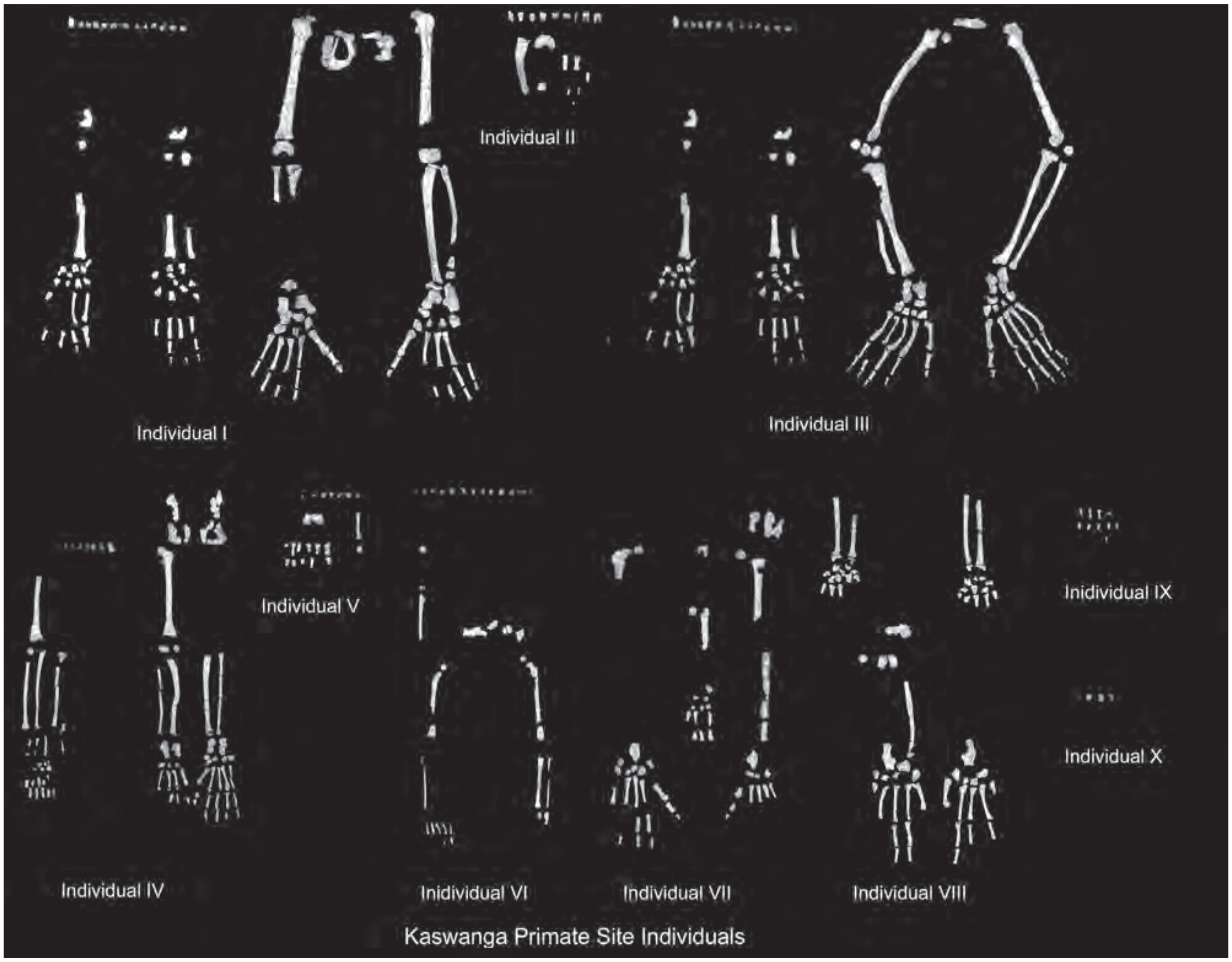

Figure 7. The Kaswanga Primate Site individuals. All to the same scale.

phalanx ray 3-4, PH17 middle phalanx ray 2, PH18 middle phalanx ray 3-4, PH29 middle phalanx ray 3-4, PH 33 middle phalanx ray 5, PH30 right terminal phalanx ray 1, PH16 left terminal phalanx ray 1.

KPS individual II – subadult male, larger than individual I

Teeth: left P_3, left M_{1-2} right M_1-$_3$, ?I^1, left M^2, right M^2.

Postcranial: R3 – distal radius, C2 – right scaphoid, PH219 – proximal hand phalanx ray 3-4, PH20 middle hand phalanx ray 3-4, PH32 terminal hand phalanx ray 1, E2- distal epiphysis of right femur, TB2 – left tibia shaft fragment, E6 - distal end of right fibula, PH 30 left proximal foot phalanx ray 1, PH22 middle hand foot phalanx ray 5.

KPS individual III – adult female

Teeth: left lower C., left P_3, left M_{1-3}, right M_2, left P^3, left M^{1-3}, right M^{1-3}

Forelimb: H5 – left distal humeral epiphysis, H6 – right distal humeral epiphysis, U6 – right proximal ulna, U5 – left distal ulna shaft, R13 – radial head, R14 – radial head, R12 – right distal radius shaft, Rll – left distal radius shaft, C15 – right scaphoid, C28 – right capitate, C31 – right centrale, C39 – right triquetrum, C44 – right trapezoid, C35 – right pisiform, C19 – right trapezium, C23 – right lunate, C13 – right hamate, C38 – left triquetrum, C22 – left lunate, C26 – left capitate, C30 – left centrale, C42 – left trapezoid, C34 – left pisiform, C18 – left trapezium, C12 – left hamate, C14 – left scaphoid, PH188 – proximal end of MC1 (mistakenly labeled in the field as phalanx), PH186 – contralateral MC1, MT42 + MT66 associated metacarpals mistakenly labeled in the field as metatarsals, PH99 – left proximal phalanx ray 4, PH100 – left proximal phalanx ray 1, PH101 – left proximal phalanx ray 5, PH221- left proximal phalanx ray 3, PH224 – left proximal phalanx ray 2. PH220 – left middle phalanx ray 4, PH222 – left middle phalanx ray 3, PH 103 – left middle phalanx ray 2, PH104 – left middle phalanx ray 5, PH105 – right terminal phalanx ray 3, PH106 – left terminal phalanx ray 5, PH107 – left terminal phalanx ray 2, PH108 – left terminal phalanx ray 4, PH 223 left terminal phalanx ray 3.

Pelvis/Hindlimb: P9 + P5 – right ischium fragment, P3 – left patella, P4 – right patella, F13 – femoral condyles, F15 – femoral condyles, F12 – right femoral head, Fll – right femur, F10 – left femur, TB7 – right tibia, TB6 – left tibia, FB6 – right fibula, FB5 – left fibula, complete articulated right and left feet.

KPS individual IV – infant

Teeth: left upper dc, left M^1, right di^1, right di^2, right upper dc, right lower dc, right dm_1.

Forelimb: H2 – right humerus (distal 2/3), H3 – distal epiphysis of right humerus, R8 - ?right radius, (distal 2/3), R10 – radial head epiphysis, R9 - ?left radius shaft, U3 – right ulna – sigmoid notch to distal end, U7 – left ulna, sigmoid notch region, U9 – left ulna shaft fragment. U* - left ulnar styloid process, C50 – left scaphoid, C51 – right scaphoid, C52 – left lunate, C53 – right centrale, C54 – left hamate, C55 – left centrale, C56 – left capitate, MT * - right metacarpals 2-5, MH22-28 – metacarpal heads, PH151 – left proximal phalanx ray 1, PH154 – proximal phalanx ray 3-4, PH155 proximal phalanx 2-5, PH161 – proximal phalanx ray 2-5, PH162 proximal phalanx 2-5, PH76 – middle phalanx ray 4, PH77 – middle phalanx ray 3, PH126 – middle phalanx ray 3- 4, PH149 – middle phalanx ray 4,PH168 – middle phalanx ray 2-5,PH170 – middle phalanx ray 2-5,PH173 – middle phalanx ray 3,PH218 middle phalanx ray 2-5.

Pelvis/Hindlimb: P8 – left ilium fragment, P5 – right ilium fragment, P10 – left ischium fragment, P12 – left pubis fragment, Pll – right ischium fragment, P13 – right pubis fragment, F7 – left femur with part of distal epiphysis, PT2 – Patella, TB4 – right tibia (no epiphyses), TB3 – left tibia TB3 with distal epiphysis, FB7 – right fibula distal end with eparate proximal piece, FB4 – left fibula and distal epiphysis, T43 – right talus, T36 – left talus, T42 – right calcaneum, T35 – left calcaneum, T37 – left navicular, T62 – right navicular, T38 – left cuboid, T39 – left medial cuneiform, T41 – left lateral cuneiform, T40 – left intermediate cuneiform, C4 – right intermediate cuneiform (field identification of right trapezoid), MT20 – right metatarsal V, MT63 – right metatarsal IV, MT64 – (?), MT61 – right metatarsal I, MT56 – left metatarsal I with epiphysis, MT57 – left metatarsal II, MT58 – left metarsal III, MT59 – left metatarsal IV, MT60 – left metatarsal V, PH109 – Left proximal phalanx ray 1, PH111 – left proximal phalanx ray 2, PH112 – left proximal phalanx ray 3, PH113 – left proximal phalanx ray 4, PH114 - left proximal phalanx ray 5, PH152 – right proximal phalanx ray 2, PH157 – right proximal phalanx ray 4, PH 115 – left middle phalanx ray 2-5, PH116 – left middle phalanx ray 4-3, PH117 – left middle phalanx ray 2-5, PH118 – left middle phalanx ray 3-4, PH 127 – right middle phalanx ray 2-5, PH216 – right middle phalanx ray 3-4, PH110 – right terminal phalanx ray 1, PH119 – left terminal phalanx ray 3-4, PH120 – left terminal phalanx ray 3-4, , PH121 – right terminal phalanx ray 3-4, PH122 – right terminal phalanx ray 3-4, PH123 – right terminal phalanx ray 5, PH124 – left terminal phalanx ray 1, PH125 – right terminal phalanx ray 2.

KPS individual V – old adult female

Teeth: left lower C., left P_3, lower molar fragment, left M^1, right M^1, ?right M^2 fragment, right M^3 .

Postcranial: E17 – distal end of right femur, MT5 – left metatarsal V, PH62, PH192, PH196 – middle hand phalanges, PH97 – right proximal foot phalanx ray 1, PH98 – left proximal foot phalanx ray 1, PH70 – proximal foot phalanx ray 2-5, PH 179 proximal foot phalanx ray 3-4, PH180 proximal foot phalanx ray 3-4, PH184 proximal foot phalanx ray 2-5, PH191 middle foot phalanx, PH39 right terminal foot phalanx, PH40 terminal foot phalanx.

KPS individual VI – infant

Teeth: right dm^1, right dm^2, left dm^2, right dm_1, leftM^1, - also tooth germs extracted from maxilla.

Note record casts and photographs were taken of maxilla and mandible pieces from which germs were extracted.

Forelimb: U4 – right ulnar shaft, proximal part, H4 – humeral head epiphysis, H8 – humerus – capitulum. PH 75 - proximal hand phalanx ray 1.

Pelvis/Hindlimb: PI 4 – right ilium fragment, P19 – left ilium fragment, P19 – right ischium fragment, P16 – left ischium fragment, P20 – pubis fragment, F8 – femoral head, F9 – left femoral neck and area around lesser trochanter, F7 – right femoral shaft with neck and distal end of femur, - assorted bits of left femoral shaft and distal end of femur, TB5 – right tibia shaft, pieces of fibula from both sides, T64 – right calcaneum, T60 – right talus (originally MH15), PH73, PH74, PH147, PH148, PH150/211, PH174 – proximal foot phalanges, PH23, PH128 terminal foot phalanges, phalangeal epiphyses.

KPS individual VII – juvenile female

Forelimb: - scapula fragment, part of spine and glenoid, R7 – radial head epiphysis, distal end styloid process of ulna, C47 – right lunate, C49 – left triquetrum, C46 - left scaphoid tubercle, C56 – right hamate, MT20 – metacarpal, MT25 – metacarpal. Four damaged metacarpal epiphyses, PH166 proximal hand phalanx ray 1.

Hindlimb: P6 – right ischium fragment, P7 – left ischium fragment, ilium fragment, F3 – right proximal femur, including neck and head epiphysis, H9 + F4

– left proximal femur – (but no neck or head), F5 – femoral head epiphysis, F6 – femoral head epiphysis, tibia fragments – shaft bits, T18 – right calcaneum, T26 – talus fragment, T30 – left navicular, T44 – left lateral cuneiform, T21 – left cuboid, T34 – left medial cuneiform, T63 – head of talus, T17 – left calcaneum, T31 – right navicular, T33 – right lateral cuneiform, MT 52 – left metatarsal I – distal end, MT27 – right metatarsal I, MT29 – metatarsal, MT30 – metatarsal, MT41 – metatarsal, MT65 – metatarsal, MT24 – metatarsal, MT28 – metatarsal, 2 metatarsals that are unnumbered, PH 90 proximal foot phalanx ray 1, PH91 proximal foot phalanx ray1, PH 88 – terminal foot phalanx ray 1, PH89 – terminal foot phalanx ray 1. The following phalanges have not yet been assigned to hand or foot. PH92 – proximal ray 3-4, PH93 – proximal ray 3-4, PH95 – proximal ray 3-4, PH175 – proximal ray 3-4, PH94 – proximal ray 2-5, PH 153 – proximal ray 2-5, PH154b – proximal ray 2-5, PH156 – proximal ray 2-5, PH167 – proximal ray 2-5, PH160/203 – middle phalanx, PH 159/214 middle phalanx, PH171 – middle phalanx, 158 – middle phalanx, PH164 – middle phalanx, PH 165 – middle phalanx, PH178 – middle phalanx, PH204 – middle phalanx, PH207 – middle phalanx, PH208 – middle phalanx, PH210 – middle phalanx, PH212 – middle phalanx, PH215 – middle phalanx.

KPS individual VIII – subadult female

Forelimb: R6 – left distal radius, R5 – right distal radius, Ul – left distal ulna with epiphysis, U2 – right distal ulna with epiphysis, C24 – right lunate (damaged), C27 – right capitate, C16 – right hamate (damaged), C40 – right triquetrum (damaged), C32 – right centrale, C43 – right trapezoid, C33 – right pisiform (damaged), C45 – right scaphoid tubercle, C26 – left capitate, C36 – left pisiform (damaged), C37 – left triquetrum (damaged), C21 – left lunate (damaged), C17 – left trapezium (damaged), C29 – left centrale, C25 – left capitate, C41 – left trapezoid , PH 69/131 – proximal hand phalanx ray 2-5, PH71 – proximal hand phalanx ray 3-4, PH181 proximal hand phalanx, PH183 proximal hand phalanx, PH185 proximal hand phalanx, PH187 proximal hand phalanx, PH 64 – middle hand phalanx, PH 65 – middle hand phalanx, PH 67 – middle hand phalanx.

Hindlimb: F14 – femoral condyles, F16 – femoral condyles, PT1 – patella, FB4 – right fibula, distal end with epiphysis, T20 – right calcaneum, T19 – left calcaneum, T22 – right talus, T27 – right medial cuneiform, T28 – right intermediate cuneiform, T29 – right lateral cuneiform, T23 – left navicular, T24 – left medial cuneiform, T25 – left intermediate cuneiform, T23 – left lateral cuneiform (note duplicated field number). MT36 – right metatarsal I, MT37 – right metatarsal II, MT38 – right metatarsal III, MT39 – right metatarsal IV, MT40 – left metatarsal V, MT31 – left metatarsal I, MT32 – left metatarsal II, MT33 – left metatarsal III, MT34 – left metatarsal IV, MT35 – left metatarsal V, PH68 proximal foot phalanx ray 3-4, PH72 – proximal foot phalanx ray 2-5, PH182 proximal foot phalanx, PH189 proximal foot phalanx, PH 190 proximal foot phalanx, PH197 – middle foot phalanx.

KPS individual IX – adult female

Hindlimb: PH66 – foot middle phalanx ray 2, PH102 – foot middle phalanx ray 5. The following middle phalanges have not been assigned to hand or foot. PH193, PH194, PH198, PH199, PH200, PH201.

KPS individual X – adult male

Teeth: right I^2, right M^3, root frag.

SITE FORMATION AT KASWANGA

It is worth emphasizing that most of this *Proconsul* material came from screening of downslope weathered sediment and soil. The site must have been deflating for many years, and it is possible that *Proconsul* fossils may have been collected here as long ago as the early 1930s. MacInnes (1943) described a poorly preserved mandible from site R5 and it is worth considering that it belongs to one of the individuals listed here. This specimen is now KNM-RU 1710, and close examination of its teeth might match it to a Kaswanga Primate Site specimen. Two of them were subadult small individuals to which we assigned no teeth.

Because most of the individuals had washed out before we found them, we do not know how complete they were at the time of burial. However, bearing in mind that we might only have excavated one subadult male, rather than two, and that more work needs to be done on identifying fragments of the collection, and taking the rest of the collection at face value, it appears that four points are worth noting.

1. Hardly any skull or mandible parts are preserved, although many isolated teeth are.
2. The proximal parts of the hind limbs are better preserved than those of the forelimbs. Foot and hand bones were often left articulated on the ends of the limb skeleton.
3. There are hardly any ribs, very few sternebrae, and not many vertebrae in this total assemblage.
4. There are hardly any other mammal fossils occurring with this one primate species here, other than the usually background scatter of fossils. Only two small lagomorph partial skeletons were found in the same general area.

These points can be taken in order. We did find small parts of skull bones and mandibles, but all were fragmentary. The mammalian fossils of the Hiwegi Formation are usually badly cracked and often distorted. Much care is needed to excavate them from the sediment, especially if penetrated by plant roots. In the case of this site, the sediments shrink when dry and expand when wet, causing even short bones such as phalanges to be broken into pieces. The large number of isolated teeth attest to maxillae and mandibles being present before deposition, in the case of Individuals I and II, and at least before erosion in the case of the others. So the lack of complete mandibles and skulls is almost certainly due to destruction either before burial or during erosion. The next two points can be taken together as they seem to be answered by Brain's (1981) carnivore feeding experiments. Baboon skeletons fed to cheetahs look like a perfect model for the Kaswanga primate remains (see Brain 1981, Figure 22a, 23e). Vertebrae (except for the tail), ribs and sternum were all preferentially consumed. Scapulae, being thinner and not as firmly attached to the torso as the pelvis, were destroyed or badly damaged. Hands and feet were sometimes eaten and sometimes not. Skulls were left intact.

Of course, cheetahs were not around in the early Miocene, but the striking similarity between what Brain's cheetahs left and what remains of *Proconsuls* here seems to point to a carnivorous mammal as the agent of accumulation. The Miocene species had no tail, so no tail vertebrae were found (Nakatsukasa et al., 2004), but otherwise the anatomical resemblance between the two anthropoids *Papio* and *Proconsul* is strong. The question of which of the several species of carnivorous mammals known from the Hiwegi Formation was the culprit in this case, is difficult. Most of the genera and species listed (e.g. in Pickford, 1986) are very poorly known—mostly from jaw and tooth fragments—(Savage, 1978) and none from associated postcranial bones. However, some of them like *Hyainailuros* are extremely large, larger than modern living felids, and big enough to swallow a *Proconsul* whole, while others, like the mongoose *Kechechia* are obviously too small. Yet another, *Teratodon*, appears to have been a specialist feeder on land snails. It is more likely that the predator was a creodont, possibly the wolf-sized *Anasinopa leakeyi* or *Isohyaenodon andrewsi,* like the one hypothesized to have carried the R114 site *Proconsul* into its hollow tree lair.

The last point concerns the dominance of *Proconsul* in the assemblage. Primates make up a high proportion of the small to mid sized mammals in the Hiwegi Formation, but there are many other taxa that could be taken by a predator. This concentration on one species that has a mean body mass estimate of about 11 kg (Rafferty et al., 1995) suggests strong prey selection on the part of a predator, rather than any other cause of death.

SUMMARY

Both the R114 and Kaswanga Primate Site *Proconsuls* seem to have been prey of a selective carnivorous mammal, probably a medium-sized hyaenodontid creodont. In the case of the former, the predator carried a carcass into a dead or dying hollow tree. In the case of the latter site the predator probably concentrated the skeletons in a burrow or narrow gully.

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